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MEMOIRS

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Case

I. THE SIGNIFICANCE OF BONE STRUCTURE.

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IT is not easy to determine who first appreciated the fact that the spongy tissue of bone is not a meaningless tangle but an architectural structure. The late Professor Jeffries Wyman read a paper "On the Cancellated Structure of some of the Bones of the Human Body" before this Society on Nov. 7, 1849. He stated that there is a reference to the matter in Ward's "Outlines of Human Osteology," which was published in London in 1838. He, however, gave the credit of first calling attention to the subject to Bourgery and Jacob (1835). Professor Wyman wrote as follows: "The cancelli of such bones as assist in supporting the weight of the body are arranged either in the direction of that weight or in such a manner as to support and brace those cancelli which are in that direction. In a mechanical point of view, they may be regarded in nearly all these bones as a series of 'studs' and 'braces.'"[1] He thought that the arrangement in some of the human bones is characteristic and has a definite relation to the erect position. "As a rule the strength of the bone seems to be obtained in other mammals at the expense of its lightness by giving greater thickness and density to the outer shell, as well as by stouter cancelli with smaller areolæ." He found but slight traces of a corresponding plan in other animals; a conclusion that seems surprising on the part of so acute an observer.

Professor Humphry drew attention to the mechanical advantage gained by the arrangement of the cancelli in his treatise on the human skeleton published in 1858.

Professor Hermann v. Meyer[2] of Zurich announced this discovery anew in 1867 and is generally looked up to as the first to grasp the idea. He certainly deserves the credit of having studied it more thoroughly than any of his predecessors. He thought that the cancellated tissue could be divided into two types, that fitted to resist pressure in one direction, and that fitted to resist it in many. The discussion was taken up with great interest by German anatomists.

[1] Boston Journal of Natural History, Vol. VI.

[2] Reichert und DuBois Reymond's Archiv, 1867.

Dr. Julius Wolff[1] applied the principles of mathematics more rigidly than had been heretofore done to the study of the bony plates. At his request Professor Culmann caused to be drawn the stress lines of a crane of the general shape of the upper end of the femur and found a surprising resemblance between the stress lines and the trabeculae. Dr. Wolff concluded that from our knowledge of the needs of a bone we can predict its internal structure and also that the converse of the proposition is true. He writes: "And thus we come to the view which, when we have once grasped it, seems so natural and self-evident, that the plan on which the bone is built is the only possible one." I make no comment on these conclusions as the discussion of this and allied questions is the purpose of the present paper.

Wolfermann[2] wrote shortly after in the same sense and included in his observations the bones of many animals. Not content with admitting the relation between the mechanical needs of the bone and its structure, he went so far as to assert that the former are actually the cause of the latter.

Aeby[3] maintained that the arrangement of the laminae of a bone depends on its movements. The laminae, according to this theory, are parallel when the axes of two connected bones remain so, but if one of these bones is flexed on the other by turning on one axis, the plates converge in the planes perpendicular to the axis. If the bones move on more than one axis there is a general convergence. Moreover, all these types show near joints a system of slightly developed transverse plates. At points of muscular insertion the muscle represents the axis of a bone.

Merkel,[4] in a paper on the femur, expressed some doubt as to the teleological arrangement of the plates, basing his objection on the striking similarity of the plan in the human heel bone which rests on the ground and that of the quadruped which projects in the air.

Bardeleben[5] published a monograph on the spinal column in man and animals which he argued is to be regarded as a trestle-work.

Langerhans[6] and Wagstaffe[7] made many sections of human bones and each concurred in the prevailing view.

Ogston[8] started the theory that plates developed from articular cartilage are perpendicular to the surface of the bone, and those from the periosteum parallel to it.

Professor Humphry[9] contraverted this, maintaining that the arrangement is not due to development, but rather has "relation to the line of weight and the direction of the forces to be resisted."

In 1882, v. Meyer[10] classified more accurately than he had done the different kinds of cancellated tissue. He recognized a round-meshed structure fitted to resist pressure in all directions. This generally presents in the middle what he calls an intermediate spongy portion, made of thicker plates and larger spaces, which adds to the strength. Then there are the short bones that receive pressure in two opposed directions and con-

[1]Virchow's Archiv, Band L, 1870.
[2]Reichert und Du Bois Reymond's Archiv, 1872.
[3]Centralblatt für med. Wissensch , 1873.
[4]Virchow's Archiv, Band LIX, 1874.
[5]Beiträge zur Anatomie der Wirbelsäule, Jena, 1874.
[6]Virchow's Archiv, Band LXI, 1874.
[7]St. Thomas' Hospital Reports, 1875.
[8]Journal of Anat. and Phys., Vol. XII, 1878.
[9]Ditto, Vol. XIII, 1878.
[10]Beiträge zu Biologie. (Bischoff's Jubilaum.)

sequently have a system in the main longitudinal. Finally, there are the shafts of the long bones, the solid walls of which break up into plates near their ends. Moreover there are plates near the ends of bones which he thinks must be considered continuations of tendons.

Roux[1] of Breslau, in a paper in which he analyzes the internal structure of an anchylosed knee, makes a further classification which, though very good, is rather long to be given here especially as it is more minute than the purposes of this paper require.[2]

That the internal structure of bone shows a well-planned architecture suited to the mechanical requirements of the part is an axiom so generally accepted that we may take it as a starting-point, although, as will appear later, it requires considerable modification. There are, indeed, many aspects to the question, which is one of no common difficulty. Although some of the most thorough of the authors mentioned above have referred to the mechanical requirements in the widest sense, it seems that many, if not most, writers have looked upon bones merely as weight-bearing appliances. Considered in this light alone the question is not a simple one. Is the arrangement of the plates that requisite when the bone is in the position of the greatest strain? If not, it is clear that there must be what builders call a large factor of safety, that is, that much more material must be disposed along the stress lines than would otherwise be necessary. Another point not to be lost sight of is that, besides the actual weight a bone may have to bear, it must be able to resist compression against the next bone to which it is subjected by muscular action.

But if we look on bones as not merely adapted to weight-bearing but as serving also for the origin and insertion of muscles, do we find the plan of the bone modified for these requirements? There seems no possibility of doubting it. The femur of a quadruped inclines downward and forward. If we suppose the upper part to be made of the least amount of bone sufficient to bear the weight, it is clear that the shaft at the neck would be thicker from before backward than transversely, as the strain comes in the former direction. But the contrary occurs: the greatest breadth is transverse. Clearly then there are other factors than the purely static needs of the bone. If this shape be for the purpose of resisting any strain it must be that of the muscles. Although, as I shall undertake to show later, certain structures occur that are in no way teleological, it is hard to believe that so important a feature as this widening of the femur should be purposeless, and we are almost forced to hold that either it is to give greater surface for muscular origin and insertion, or that it is to resist lateral tension from muscular action, or that the two reasons coëxist.

The precise part played by muscles is extremely difficult to determine. With them it is proper to associate ligaments, there being no doubt that what is a ligament in some animals is a muscle in others and, moreover, it seems a matter of no consequence whether the strain is applied to a bone by the pull of a muscle on a tendon or less directly by making tense a ligament. There seems no doubt that a factor in the shape of bones, besides weight-bearing, is muscular attachment. Clearly a large muscle must have a

[1]Beiträge zur Morphologie der functionellen Anpassung. Archiv für Anat. und Entwick., 1885.

[2]It is not thought necessary to discuss what has been written on the growth of bone nor on the arrangement of the cancelli in pathological conditions.

sufficiently extended surface of origin, and again it is necessary for leverage that many muscles, at least, should be attached to projections. We find, therefore, that the whole shape of a bone is determined so as to meet other than the static requirements. As for processes like the trochanters no one denies that they serve for muscular attachment. I have elsewhere[1] published some notes on the structure of bone beneath processes for the insertion of muscles and ligaments. In some cases, notably when the process is very small, like the anterior inter-trochanteric ridge of the femur, the shaft is continued beneath a layer of cancellated tissue. When the process is larger the surface of the shaft seems to go round it rather than under it. The shaft is sometimes, but by no means usually, found continued under the tubercle of the human radius and the coronoid process of the ulna. It is sometimes represented by plates recalling the process which Bigelow[2] has named the "true neck of the femur" which, when very well developed, appears to represent the posterior wall of the neck continued beneath the lesser trochanter. As a rule, however, there is no well-marked separation of the cancellated tissue of any of the larger processes from that of the main bone beneath. The third trochanter of the horse (fig. 1) is a striking instance. One would be inclined to look for a continuation of the shaft beneath it to support the weight, but such is not the case.

It being then admitted that the shape of bones shows provision both for a sufficient extent of muscular origin and for tendinous insertions it remains to see what internal arrangement of the laminae is found in the processes. Of course in cases where what would be the shape of the bone, were static needs the only ones, has been modified to admit of a larger space for muscular origin, it follows that the internal structure must also of necessity be modified; but an important and difficult question is whether the internal structure shows any special arrangement to resist the pull of the muscles and whether any of the bony plates are continuous with tendinous or ligamentous insertions. I am strongly inclined from the study both of sections of dry bone, and of bones decalcified with the soft parts unremoved, to reply to both questions in the negative. Ligaments and tendons are, I believe, never inserted at right angles to the surface of a bone. They spread out over it, being inseparably united with the periosteum and in some cases with cartilages. Thus the strain is diffused over a larger surface. It is very remarkable to what thin surfaces and to what weakly supported ones powerful muscles are attached; familiar instances are the tuberosities of the humerus and the trochanters of the femur in man. The cancelli inside of these processes are light and seem arranged to support the delicate shell of bone and not to resist muscular action. In some few places, as for instance at the back and underside of the os calcis, there are series of plates that seem to represent fibres from the tendo Achillis and the plantar ligaments, but I have not been able to satisfy myself of any continuity in decalcified specimens. Be that as it may, such systems are exceptional.

To sum up to this point it appears that the shape of the bone depends not solely on its needs as an organ of support but also on its needs as a fixed point for the origin and insertion of muscles. Further, that although this modification in shape must necessarily demand a change of the internal architecture, yet this change is only what is requisite

[1] Remarks on the Position of the Femur and on its so-called "True Neck." Journal of Anatomy and Physiology, Vol. IX, 1875.

[2] The Hip (Philadelphia, Henry C. Lea) 1869; also The Boston Medical and Surgical Journal, 1875.

for the support of the bone under the changed conditions and that the strain of the muscles being diffused over its surface the internal structure shows no special adaptation to meet it. Finally, that, in some few cases, there are apparent exceptions to this last rule.

We have so far considered an individual bone as if it were simply a piece of a machine which, to fulfil its function, must have a certain size and shape and a certain power of resistance. Other and broader questions now present themselves.

We know that certain classes and orders of animals have a characteristic structure of bone of which the most striking instances are the slender bones of fishes and the expanded bones of birds. The same is true of certain orders of mammals; but we do not know just how far such characteristic structures can be ascribed to genera or to species. That these peculiarities are in general advantageous may be considered as accepted, but are they always so? Do they extend to every bone of the skeleton? Are useless or rudimentary structures found in bone? Do particular bones show a similarity to corresponding bones in other animals, and if so, is the structure in each case solely teleological? In fine is there ground for Wolff's assertion that a bone is built on the only possible plan?

It was the writer's intention originally to limit the discussion to mammalian bones, and this plan has been followed in the main, but he has been led in one or two instances to refer to those of other classes.

Let us now pass in review, the proximal ends of the humerus and femur of a number of mammals, beginning with man, and having compared the bones of the two extremities in the same species together, then compare each with the corresponding bones of other animals.

MAN. These bones have been so often described, that a summary sketch shall suffice. In the humerus (fig. 2) the shaft is thin, the spongy tissue light and its plan very indistinct. It is denser in the head where it is of the round-meshed pattern. It is very light in the greater tuberosity. Sometimes a system of plates running up into the head from the inner side of the shaft can be made out. The femur (fig. 3) is of a much heavier make, the shaft is much thicker and the plan distinct. In brief, this consists of decussating plates from either side of the shaft, of a very well marked series, running from the lower side of the neck into the dense, round-meshed head, of a series of arches from the outer shaft which meet and perhaps pass through this series, and finally of the light tissue in the trochanter major with a few plates parallel to its surface. The important differences between the bones are the rudimentary neck of the humerus, its much lighter structure and indistinct plan. The teleological significance is evident.

APES. The humerus of the *chimpanzee* (fig. 4) might easily be mistaken for a small human one, its chief difference being a greater density of structure. The femur (fig. 5) is on the same plan as in man. The tissue of the head is very dense. Its centre is almost solid bone. The bones are larger in the *gorilla*. The humerus (fig. 6) is a little broader and the series of plates running to the head from the inner side of the shaft is more defined. The femur (fig. 7) is very like the human one, but below the trochanter the shaft is convex. The head is very dense. In both these animals the femur is much denser and heavier than the humerus, though the difference is less than in man. It is hard to say whether the difference between the two is greater in the chimpanzee or the gorilla. In the *mandrill* the humerus (fig. 8) is broader, the plates from the shaft show

a decussation and the series from the inner side to the head is more distinct. In short, it is more like a femur. The bones of *monkeys* differ from those of man and the higher apes by their greater lightness. The cavity in the shaft is relatively larger and reaches nearer the ends.

Carnivora. I have examined the bones of the *dog*, *lion*, *otter* and *sea otter*. No detailed description is necessary. The humerus and femur are more alike than in man and the apes, the neck being relatively longer in the humerus and shorter in the femur than in the latter order. There is the same general plan in humerus and femur. The head of the latter shows a somewhat greater solidity than in the former. This difference was especially marked in the dog and hardly perceptible in the sea otter. This animal was chosen in order to ascertain whether the bones present any resemblance to those of the seal. Unfortunately, I could examine but a single sea otter and the bones proved immature and consequently unsatisfactory, for typical structure is usually evident only after the union of the epiphyses.

Pinnipedia. The bones of the *seal* are very interesting. The section of the humerus (fig. 9) passes through the head and the inner[1] tuberosity. It shows plates leaving both sides of the shaft and tending towards the middle. Others pass into the head from below. The line of the epiphysis of the head is well marked and probably the line obliquely cutting off the tuberosity marks the epiphysis also. The head is of a light, round-meshed structure. The greater part of the tuberosity is taken up by plates, radiating from two solid masses, situated, respectively, on the upper and outer border, which, meeting at its outer extremity, form with the attached base a triangle, inside of which is some light, spongy tissue. The femur (fig. 10) is by no means very different, but less distinct. It shows a head of no greater solidity than the humerus. In both bones we find a structure differing from any that we have yet seen, consisting of broad, relatively thick plates with large spaces between them, which appears to be a generic peculiarity. This description is made from bones of the *P. vitulina*, but the figure of the femur is taken from the *P. Groenlandica* which corresponds strikingly. The humerus in *Otaria jubata* shows a denser structure in the head and the characteristic structure of the seal is less evident, though there is an approach to it. As above stated, the bones of a young sea otter showed no trace of this peculiarity.

Cetacea. I have examined bones of small *whales* fifteen or eighteen feet long, probably the *Globicephalus melas*, and also of *porpoises*. The section (fig. 11) embraces the whole humerus. The denser, spongy tissue of the head is distinguishable. Plates from the thick inner side run into it, and then there is a beautifully marked decussation at the upper end of the bone of plates from either side. The highest ones from the outer side run to the top of the bone. The tuberosity is of lighter texture. The thickening of the solid parts on each side near the middle of the bone is even more marked in a similar section of a young porpoise. The structure is very dense, and consists of thin plates arranged very closely together. It seems characteristic.

Ungulata. I have examined bones of the *horse*, *moose*, *gazelle*, *caribou*, *sheep*, *goat* and *hartebeest* (an African antelope). The four first-mentioned species differ from the last-mentioned three in having the cancellated tissue prolonged much further into the

[1] This section through the inner tuberosity shows, I think, a greater resemblance to the rest of the series than one through the outer, owing probably to the curious formation of the humerus in this animal.

shaft of the bone. The *moose* (figs. 12 and 13) is a good example of the former type, and indeed it is an excellent specimen of the structure in the quadruped. The internal structure is as similar as the difference in shape between the humerus and femur allows. There is very little difference in density between the heads of these bones in the same animal. I have been able to cut only the femur of *Rangifer tarandus*, the caribou. The structure of the head is very dense, decidedly more so than in the femur of the *moose*. The plates in the neck are very delicate and near together, giving the bone rather a characteristic appearance. The bones of the *hartebeest* (figs. 14 and 15) are very striking. The walls of the shaft are very thin in proportion to its diameter, and there is no cancellated tissue below the very ends. This is pretty dense in the heads and lighter in the tuberosity and trochanter. A series of plates can be traced from the inner side of the shaft into the head. Both bones, but especially the humerus, present large plates and bars running through empty spaces, giving very much the appearance of a bird's bone. As it was known that this animal had died in a menagerie, it seems possible that the bones are pathological, but both the *sheep* and the *goat* show in a less degree the thin shaft and the absence of cancellated tissue in parts where it is found in the other ungulata that I have examined.

MARSUPIALIA. In the *kangaroo* the humerus is much smaller than the femur, and the plan not very clear. The femur (fig. 16) shows the usual plan; but these bones present one remarkable peculiarity. In the bones hitherto described the surface of the head is always of spongy tissue and the line of the epiphysis when visible cuts off a considerable portion of the head. In the femur of the kangaroo the line of the epiphysis separates a crust of solid bone covering the head. This crust seems precisely as compact as the bone of the shaft. In the humerus there is a similar arrangement, only the outer portion of the crust shows a number of small holes, an approach to spongy structure. Anxious to know if this is a marsupial peculiarity, I examined the bones of the *opossum* and found precisely the same hard cap constituted by the epiphysis in the femur, but in the humerus the epiphysis consists of spongy tissue.

To study the general plan of the heads of these bones we should begin with a quadruped. We find in the humerus and femur a system of plates passing off from the outer and inner walls of the shaft and forming Gothic arches at the top of the bone. The head is of dense, spongy tissue, of the round-meshed pattern, into which runs a series of plates from the underside of the neck. The great tuberosity and trochanter are made of looser tissue. In the former, the plan is less certain; in the latter, it is in the main, (as seen in frontal plane) a rectangular network of vertical and horizontal plates. Externally there may be a series parallel with the surface. In most of the animals mentioned, this general description will apply to both humerus and femur. The head of the humerus is of about the same consistency as that of the femur in ungulata, in which the weight is about equally distributed between the bones, and in the seal, in which neither bone bears any weight. In the carnivora, in which the anterior extremity is more prehensile, the head is lighter and this difference is still more evident in apes and man. In the apes we find a lengthening of the neck in the femur and a shortening of that of the humerus, with a corresponding change in the internal structure.

Reserving till later a discussion of several questions, we may make from this series of specimens at least the general conclusion that these homologous bones of the two extremities of the same animal correspond closely in structure when their function is nearly the same, and that when their function is different their structure differs also but that the main features of the common plan can still be recognized.

The study of the calcaneum and the olecranon is very instructive. A longitudinal section of the human heel bone (fig. 17) may be described as follows: There is a thickening, from which plates radiate, situated at the lower border of the upper articular surface. Some go forward to the plate that rests against the cuboid, others downward, others backward and downward, the latter being joined by other plates arising above the point mentioned. There is then a series of plates acting as ties passing from the posterior towards the anterior surface describing a curve with a downward convexity. These plates come very near to one another at the under surface of the bone. The whole structure may very aptly be compared to a triangular rafter even to the appearance of a vacant space in the middle at the neutral point. Besides these systems there is often seen a series of plates parallel to the posterior surface held to be continuous with the fibres of the tendon.

This structure is so admirably adapted to the upright position that it seems very surprising that a strikingly similar arrangement should be found in the os calcis of quadrupeds in which its position is utterly different, the hind end pointing upward in the air instead of resting on the ground. Merkel uses this as an argument against the teleological significance of the internal structure of bone, and it long seemed to me an almost insuperable difficulty; but in fact, rightly interpreted, it is a strong argument on the other side. Let us suppose a man in the act of running with one foot in the air and the whole weight of the body resting on the toes of the other. The heel is raised and the foot is in the position of a quadruped's. Most of the weight is, of course, transmitted through the leg to the os calcis and it may be divided into two components, one running forward to the cuboid, the other backward to the tuberosities of the bone. These no longer rest on the ground and the pressure conveyed to that end of the bone is resisted by the tense tendo Achillis, so that the conditions are essentially the same in running and in standing; only of course there is a far greater strain in the former position which is the one normal to quadrupeds.

The bone in the *chimpanzee* (fig. 18) is very like the human one but the series of plates that runs backward does not appear to reach the inferior surface of the bone.

In the plantigrade bear (fig. 19) the bone is relatively longer, but the principal new features it presents are the greater thickness of the upper and lower surfaces. In the lion (fig. 20), horse, deer and gazelle the bone is more elongated, but the same general description will apply to all. In the seal (fig. 21) the bone is not used to bear the weight of the animal but for purposes of propulsion in swimming. The contraction of the muscles presses it against the astragalus and the line of pressure divides as in the other animals. We find, therefore, an essentially similar plan of internal structure. The thick lower border is seen to be composed of many of the laminae of the inferior system which meet at this place. The structure of the bone is lighter than in most of the other animals mentioned, but the characters of the seal are less distinct than in the long bones or the vertebrae.

At first sight it would seem that in man there is little in common between the olecranon and the calcaneum. It is possible, however, to recognize in the very delicate spongy tissue of the human olecranon (fig. 22) two systems that pass upward crossing each other in a series of graceful curves. The best marked comes from the posterior border, the other from the articular surface of the great sigmoid cavity. In the *gorilla* we have the same thing only the scale is larger and the plates stronger. The plan is such as we find in many other prominences.

Now in the lion we have an example of the arrangement common in quadrupeds in which the olecranon, pointing upward just like the os calcis, has a strong tendon implanted at the extremity in the same way and transmits the weight to the shaft of the bone as the os calcis transmits it to the tarsus. The teleological relations are strikingly similar. The main difference is in the point last mentioned, that in the os calcis there is a series of plates running downward and forward against the surface for the cuboid and that in the ulna the pressure is transmitted through the shaft. In the *lion* (fig. 23), which may do for a type, there are found in the elongated olecranon, two series of plates crossing one another at the back strikingly resembling the calcaneum, and we find that the compact substance of the back of the shaft is formed by the aggregation of many distinct plates. In the *bear* the shape of the olecranon is peculiar. It is pointed and quite different from the rather human heel bone but the internal structure shows a decussation of plates. In some of the ungulata the shape as well as the internal structure is very similar. I think that in many cases it would be very difficult to tell whether a section, which one could not compare with others, were through the end of the olecranon or the end of the calcaneum.

This series shows, therefore, a similarity of structure coincident with similarity of function in non-homologous bones and the presence of the general plan throughout the series.

We shall next examine the vertebrae and more particularly their bodies. The essential features of the body of a mammalian vertebra are a series of longitudinal plates running from one end to the other and a series of weaker plates crossing them at right angles especially developed near the ends. The surfaces of the pedicles are almost always thick. They give off plates that in sagittal sections are sometimes seen joining the transverse system and in other places describing curves and joining the longitudinal. Sections parallel to the intervertebral discs show at times series of loops from the pedicles across the body decussating with similar ones from the opposite side.[1] These are probably formed in part by the cut edges of longitudinal plates. The chief system in all mammals is the longitudinal one.

In *man* (fig. 24) one is struck by the lightness of the whole structure. The plates are nearer together at the ends and wider apart at the centre, where they are thicker. This may serve for a centre of support and also form the walls of the vascular canals. Something may be seen of the oblique systems, but they seem too weak to be of much use.

The same general description may apply to the *lion* (fig. 25) and the *dog;* but the plates are nearer together and the formation is denser, there being little space in the middle. In the *horse* (fig. 26) again the essential system is a dense longitudinal one.

[1] The reader will find much that is interesting and valuable in Bardeleben's monograph on the spine already referred to.

The longitudinal arrangement is evident in the seal (fig. 27), but transverse sections of the lumbar vertebrae show the plates diverging from the compact bone on the inner side of the pedicle with remarkable clearness. There is also a set running horizontally inward from the lower surface of the transverse process which arises from the body of the vertebra. These vertebrae present another peculiarity: to wit, the great thickness of the epiphyses at the ends of the bodies which consist of cancellae arranged longitudinally. This description applies to the *Groenlandica* as well as to the *P. foetida*. In one or two dorsal vertebrae of the *Otaria*, which I had an opportunity to examine, the longitudinal system was clear and the transverse indistinct. In all these there were the thick plates and large spaces which are characteristic of the seal tribe.

The vertebrae of *cetaceans* show the characteristic structure of many thin plates very close together. The arrangement is clearly longitudinal with tubular spaces. In the dorsal region the structure is very dense and heavy, the middle of the body in a small whale being almost solid bone. The structure is lighter in the lumbar region and in the caudal lighter still. The systems of horizontal plates from the transverse processes can be traced but a short distance in the body. The lumbar vertebra of the whale (fig. 28) has one peculiarity that I have seen in neither carnivora nor ungulata, namely, a solid crust of bone surrounding the body. The upper one is continuous with the compact tissue of the pedicles, the lower with that of the transverse processes. In the dorsal region this solid shell is found only at the upper side of the vertebra bounding the canal. I have not found this in either the dorsal or lumbar region of the porpoise.

I have had the opportunity of cutting but one bone of the *Sirenia*, one of the anterior lumbo-caudal vertebrae of the manatee (fig. 29). The structure is very whale-like. It has the same plate surrounding the body as in the same region in *globicephalas;* the same decussation of the plates from the transverse process on each side; a *substantia intermedia* and at the lowest part a structure of coarser plates and larger spaces. Above this on either side of the middle the structure is denser than in the lumbar vertebra of the whale.

Summing up our observations on the bodies of the mammalian vertebrae we find that the plan is in the main a longitudinal one. In man, the structure is the lightest of all; in whales and the manatee the heaviest. There can hardly be a doubt that the pressure to which the bodies of the vertebrae are constantly subjected is in an antero-posterior direction being due to the compression they exercise one on another. In quadrupeds the dorso-lumbar region may be compared to a bridge,[1] one end of which is supported on piers (to wit, the femurs), the other being suspended (from the scapulae) sometimes only by muscles, sometimes having the additional support of a clavicle. The thorax is suspended by the serratus, the neck by the levator anguli scapulae and therefore the thoracic spine is supported through the ribs. The pieces of the spine are connected by strong longitudinal ligaments; many and powerful muscles, by their contraction, press the vertebrae together, hence the longitudinal arrangement of the plates, for it is necessary to the safety of the arch that it should be compressed. In man, the arrangement is different. The spine is placed on end and really requires less strength than in the quadruped.

[1] Compare Lucae; Robbe und Otter. Abhandlungen des Senckenb. naturf. Ges., Bd. VIII and IX.

In whales the conditions are not quite the same; nevertheless the spine is not straight but bent in the thoracic region. The shape of the bodies of the vertebrae is not such that this could be done without the restraining force of ligaments and the vast power of the muscles must pull the vertebrae together; hence, here also the longitudinal arrangement.

In the seal the plan is less modified. It has been stated that the pressure is transmitted to the thoracic portion of the spine through the ribs and very probably this occurs through the tubercle that articulates with the transverse process much more than through the head of the rib. Hence the pedicles connecting the transverse processes with the body must be strong. But this is not the only reason; the pedicles have also to transmit the strain, probably very considerable, occasioned by the pressure on the articular processes in various movements. Thus the firm walls which the pedicles usually present are what might be expected, and it is natural enough that plates should pass off from these points of support through the vertebral bodies both lengthwise and crosswise. Still, as a rule, the work done by these systems does not seem important. Before approaching some other questions, it may be interesting to take a cursory view of the vertebrae of other classes.

In the osseous fishes (fig. 30) the body is doubly concave. The end plates are supported by others running antero-posteriorly which appear as radiating lines in a transverse section. These are connected by occasional transverse plates which in some places are so developed as to suggest concentric rings.

In the alligator (fig. 31), the plan bears a certain resemblance to that of the fish. There is a general radiating arrangement with mostly large interspaces. Near the upper part of the body, *i. e.*, just below the canal, the structure is thicker. The cancellous tissue is very dense in the rounded end. Longitudinal sections show plates running from before backward and also near the side, strong plates running downward and backward from the anterior articular processes, and others downward and forward from the posterior ones. There is a beautiful strong system of plates with large interspaces in the arches and roots of the transverse processes that is very characteristic.

In the great Galapagos tortoise a cervical vertebra shows a plan of rather thick plates and large interspaces. The osseous tissue is much less dense than in the alligator. The vertebra cut being the only cervical one in the series, it is not worth while to discuss the arrangement in detail as it cannot well be compared with the others. Suffice it to say that the plates are disposed chiefly longitudinally, and that the general appearance is not in the least like that of the alligator.

The vertebra of the snake is curious, presenting more solid substance than any vertebra I am acquainted with. Figs. 33 and 34 represent two frontal sections made respectively near the back and front of the body of a vertebra of a pithon. Fig. 34 is just behind the hollowed anterior end. The circular portion of spongy tissue is just back of the cup and is inclosed by an envelope of compact bone. The latter is found also at the lowest part of the body and in the articular processes which receive the posterior ones of the vertebra in front. The other section shows almost exclusively solid tissue both in the body and in the posterior articular processes. Fig. 32 shows a horizontal section through the body. The spongy tissue on the convex head is well shown; that in

the cup is seen better at another level. We see here the section of a median vertical plate extending from the cup of compact tissue at the front, back to the head where it breaks up into trabeculae. There is a band of spongy tissue running from the articular surface for the head of the rib obliquely backward and inward. It may be that elasticity is gained by the constituent parts of the ball and socket joint at the ends of the bone being made of spongy tissue, which transmits the pressure to deeper solid bone. The articular processes that fit into one another are remarkably solid while the articular tubercle for the head of the rib is cancellated. Fig. 35, showing a frontal section of a dorsal vertebra of a bald eagle, makes a description superfluous. There is a general resemblance to the dorsal vertebra of an alligator that is very striking. If we compare this highly specialized type with the vertebra of a peacock that flies but little, at the first glance the difference appears very slight, but with a little study the wonderful lightness of the plates in the eagle becomes apparent. Let us now put together the conclusions that seem justified by this series of studies of bones.

We started by accepting as established, that the structure of bone both external and internal, is, in general, correlated with the strain it has to resist, but we found that its external shape is modified so as to give room for the attachment of muscles. The internal structure is not modified to resist the pull of the muscles, except in some few instances, and the fibres of tendon are not continuous with the fibres of decalcified bone.

We find also that the strength of the osseous structure increases with the strain on the bone. Thus the trabeculae of the human humerus are lighter than those of the femur, while in the ungulata they are nearly equal, and the lumbar vertebrae of the whale are intermediate in density to the dorsal and caudal ones.

We find a marked correspondence of structure between homologous parts of bones having nearly the same function, as the proximal extremities of the humerus and femur of the ungulata; and where the function is diverse there is a corresponding difference of structure, as shown by the shorter neck of the humerus and the longer neck of the femur in man and the apes, the traces of the common plan being recognizable.

We find a similar correspondence between non-homologous bones having a nearly similar function, as between the olecranon and the end of the calcaneum in many quadrupeds.

The study of sections of different bones in the same animal, and my observations, are by no means limited to the parts discussed in this paper, shows that certain classes, orders and genera have a characteristic type. The main characteristics of the bones of fishes and birds are too familiar to require mention, and I have not given enough study to reptilian bones to discuss them in detail. Among mammals we find a characteristic structure in the pinnipedia, and another in the cetacea. We find a considerable difference among the ungulata. These features are more marked in some bones of the same skeleton than in others. Beside these peculiarities of the skeleton as a whole, there are occasional appearances that are characteristic of certain animals. Are these teleological?

To consider first the outer shape of the bones, it is hard to believe that the needs for support and motion should be so much alike in the horse and rhinoceros and so different from those of the even-toed ungulata, that the former should require a third trochanter,

and that the latter should not. It is very problematical whether the supra-condyloid foramen of the humerus is of advantage to its possessors, and if so, that it would not be equally useful in species that do not possess it. Why is there a supra-condyloid foramen in the humerus of the seal and none in that of the sea lion? The solid epiphysis of the head of the femur in the kangaroo is not easily accounted for. If it is said that it is to resist the shock of the forcible extension of the femur in jumping, one might ask what explains its appearance, in a less developed form indeed, in the little used anterior extremities, or why it is found in the femur of the opossum. To say that this structure is the result of heredity, gives no explanation of its original appearance. If it is useful one would expect to find it in other leaping animals.

The occurrence of apparently useless rudimentary structures in other systems is so well recognized that there is no *a priori* reason why they should not occur in bones. Professor Heiberg[1] of Christiania has the merit of showing that the lines on the lower end of the human femur, erroneously supposed to be due to the pressure of the semilunar cartilages, are of this class, being, in fact, the representatives of the more marked separations of the patellar and the two condyloid surfaces in many animals. It is not unlikely that many features of the internal structure of bone may have this significance.

It is curious that the two most striking peculiarities of the texture of bone that we have noticed in mammals, are those of the seal on one hand, and whale tribes and the manatee on the other. These aquatic animals resemble one another in the thick layer of fat under the skin and in the flipper-like anterior extremities, though these are rather rudimentary in the whale and highly specialized in the seal, the former having relatively weak muscles and the latter strong ones; but the bones, or at least the larger ones, differ radically in these two types. Each departs from the ordinary plan in an opposite direction, the seal having thick plates and large interspaces; the whales and manatee, very numerous thin plates crowded together. It may be urged that the purpose of the heavy cetacean bone is to resist pressure at great depths, but though this need may exist for the larger whales, it probably does not for several species, and certainly not for the manatee. The bone being then apparently unnecessarily massive in the whale, the architectural plan of the internal tissue seems doubly unnecessary, yet we have seen it beautifully marked in the whale's humerus. In the manatee, especially, there is a strong suggestion of a degenerating type. On the other hand, the structure of the bones of the seal implies at once strength and lightness.

It appears, therefore, evident that so far from the actual structure of the bone being the only possible one, it in many cases presents useless features, and that certainly there must be some determining factor besides teleology. Is it impossible to hold that the vertebrae of an alligator, for instance, could not answer their purpose equally well if the internal structure were more on the plan of mammalian vertebrae? Are there not peculiarities of race that in all cases, at least, do not answer any definite purpose? It seems to me that there can be no reasonable doubt on the matter. It may be urged that we lack the knowledge to decide whether any given organism considered as a whole is or is

[1] Archiv. für Anat. und Entwickelungsgeschichte, 1883.

not as good as its nature admits. It may be urged that an essential element of perfection is the due proportion of parts and faculties, and that it is impossible for us to say that greater development in some particular direction would be for the welfare of the individual. I have no desire to dispute the great truth underlying these propositions, but in view of rudimentary organs alone, it would appear that at least in some subordinate details useless structures occur, and we have no means of deciding what limits to assign to the action of the causes producing them. It is certain that these appearances are not due to chance; there must be some determining cause modifying the structure in this direction. It is customary now to quote rudimentary organs and anatomical anomalies as evidences of descent, but it seems to me very improperly, occurring as many of them do quite out of the line of inheritance. This criticism applies with greatest force to anomalies, but rudimentary organs seem phenomena of the same general class. What principle then shall account for them? We must turn to homologies. We see throughout vertebrates a general plan; and though great modifications occur, the plan persists. No liberties, so to speak, are taken with it beyond a certain point. There are, never, for instance, more than two eyes, or one mouth or four pairs of limbs. Is there reason to be sure that none of these, or analogous modifications, might not be for the benefit of the individual? Yet, I think every student of natural history would look on the suggestion that they will ever occur as chimerical.

The principle of homology has a restraining influence on variations of structure, both in quasi-accidental instances, as in anomalies, and in transformation, of species (if that occurs) by restricting changes within the limits of the general plan.

To condense further these deductions, it appears that the internal structure of any particular bone may show evidence of three factors: first, that of teleology; second, that of homology; third, that of correlation to the structure of other bones of the same animal. The relative prominence of these factors varies greatly. For example, in the humerus of the whale the first is of little moment and so is the third in the heel bone of the seal. Thus, while we find provision for the fitness of the part, we find also sometimes apparently useless structures, sometimes apparently evidences of degeneration, but throughout are more or less distinct marks of harmony with other parts, and of homology with other forms. How has this been accomplished? Clearly the crude notion that accidental, purposeless, external forces should be sufficient to change by slow degrees one such organism into another of a different species is untenable. The doctrine of chances alone shows it to be impossible. There is, moreover, the unanswerable argument of the inevitable uselessness of incipient structures. Where we see the need, we see the structure to meet it already perfect. We see also the combination of homology with teleology. Whatever, therefore, the share of evolution may be in the production of species, it is not one of chance. The changes must be for the most part comparatively sudden, and, therefore, due to an implanted, internal force acting in predetermined directions. On the theory of external accidental forces, the preservation of homology is incomprehensible. The action, however, of this internal force, is, no doubt, modified by accidental secondary causes, which may produce degenerative as well as progressive changes.

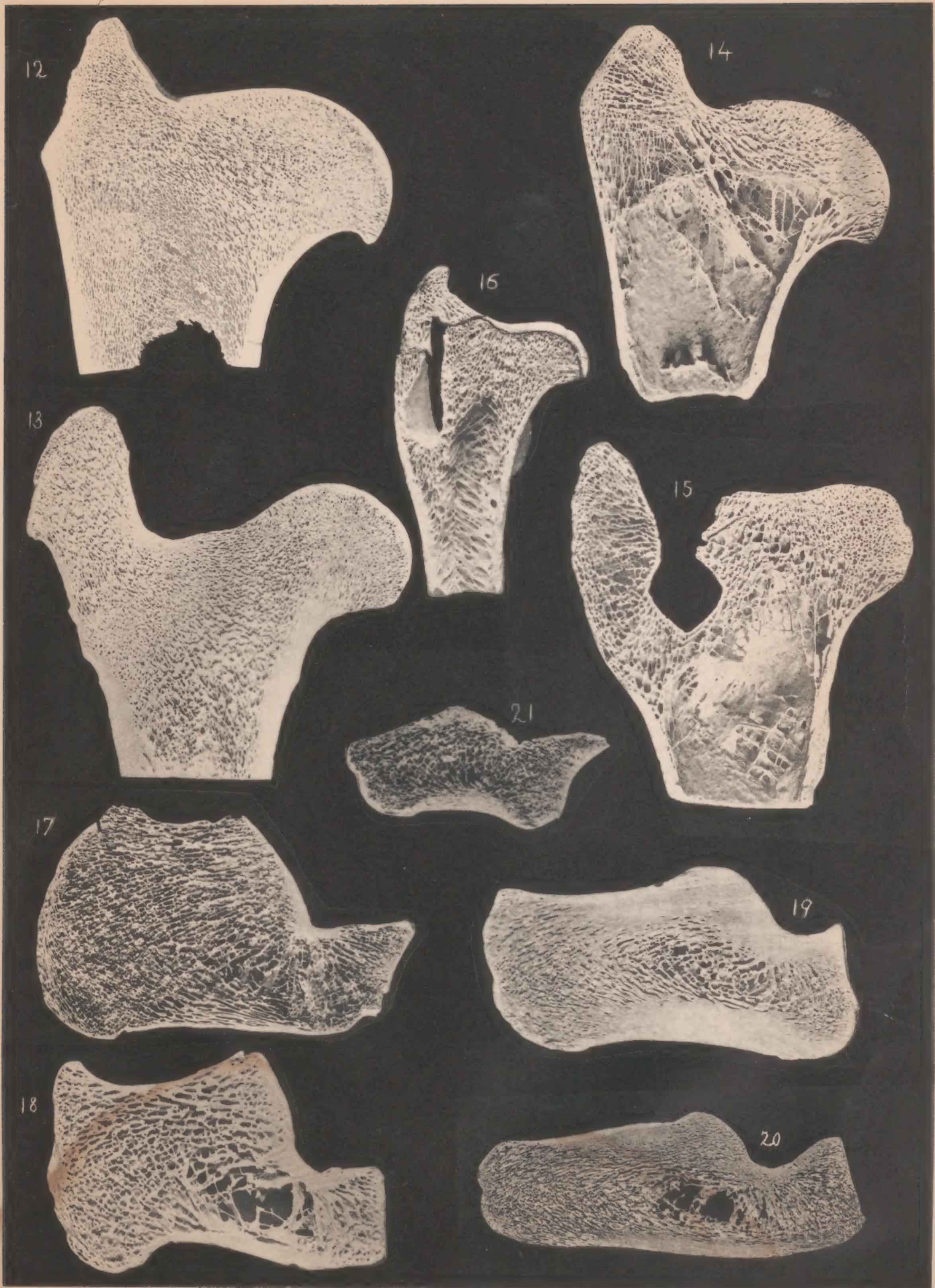
In conclusion, I wish to express my sincere thanks to the authorities of the Boston Society of Natural History and of the Museum of Comparative Zoology at Cambridge, for their kindness in allowing me to cut valuable bones. I am indebted for many of the best sections to the skill of Dr. S. J. Mixter, Assistant Demonstrator at the Harvard Medical School. The illustrations are phototypes by the Lewis Company made from photographs taken in every case from the actual specimen.

DESCRIPTION OF PLATES I-III.

Fig. 1. Femur of horse, cut through third trochanter.
" 2. Humerus of man.
" 3. Femur of man.
" 4. Humerus of chimpanzee.
" 5. Femur of chimpanzee.
" 6. Humerus of gorilla.
" 7. Femur of gorilla.
" 8. Humerus of mandrill.
" 9. Humerus of seal (*Phoca vitulina*).
" 10. Femur of seal (*Phoca groenlandica*).
" 11. Humerus of whale (*Globicephalus melas?*).
" 12. Humerus of moose.
" 13. Femur of moose.
" 14. Humerus of hartebeest.
" 15. Femur of hartebeest.
" 16. Femur of kangaroo.
" 17. Calcaneum of man.
" 18. " " chimpanzee.
" 19. " " bear.
" 20. " " lion.
" 21. " " seal.
" 22. Olecranon of man.
" 23. " " lion.
" 24. Vertebra of man.
" 25. " " lion.
" 26. " " horse.
" 27. " " seal (*Phoca foetida*).
" 28. " " whale (*Globicephalus melas?*).
" 29. " " manatee.
" 30. " " horse mackerel.
" 31. " " alligator.
" 32. " " pithon (horizontal).
" 33. " " " (frontal, near posterior end of vertebra).
" 34. " " " (frontal, near anterior end of vertebra).
" 35. " " bald eagle.

THE LEWIS CO. BOSTON.

DWIGHT, STRUCTURE OF BONE.



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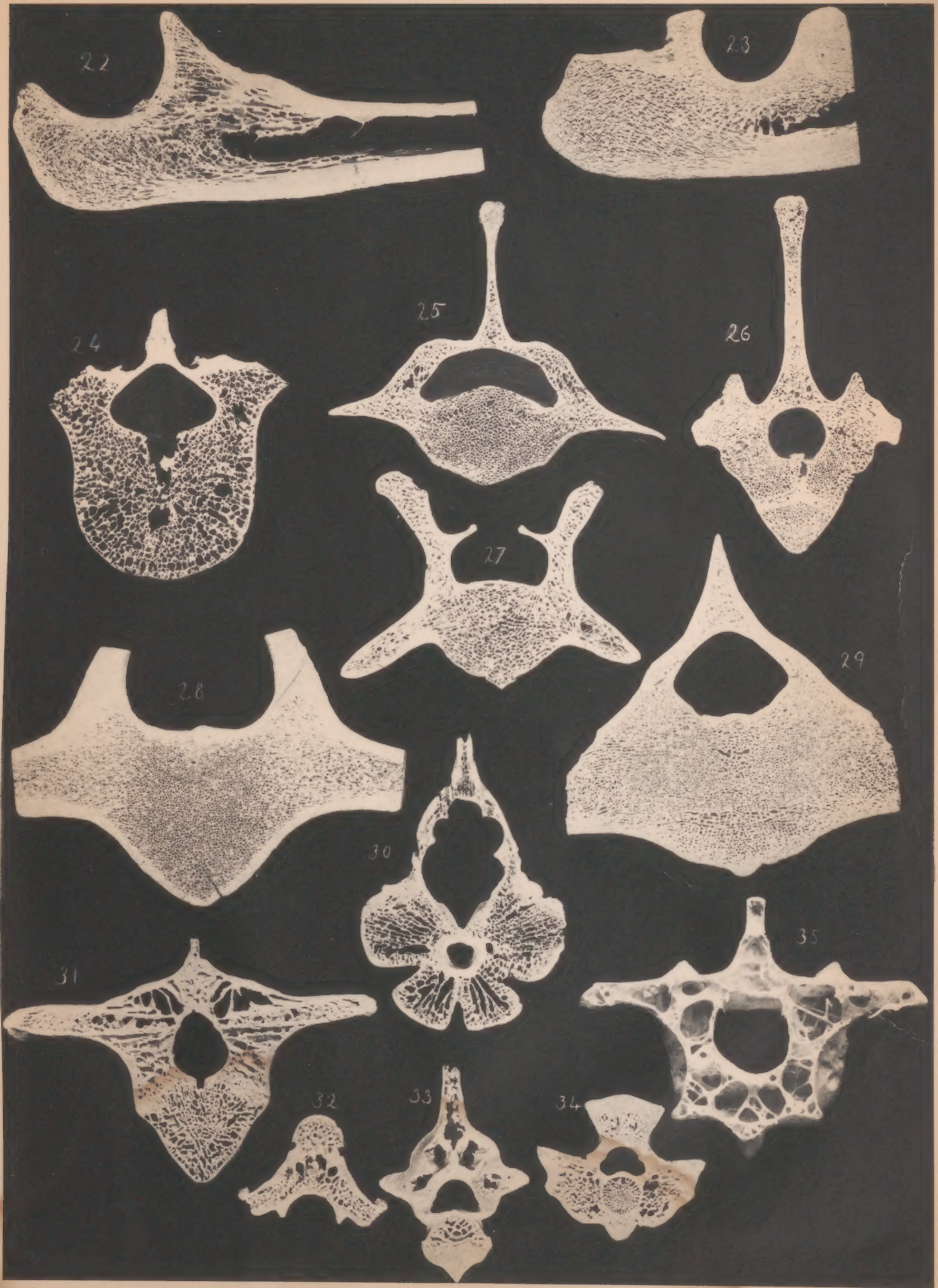
DWIGHT, STRUCTURE OF BONE.



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